PHYSICAL CONTROLS OF NITROGEN SUPPLY IN EARLY SUCCESSIONAL RIPARIAN ECOSYSTEMS ALONG THE TANANA RIVER, ALASKA

By

Nicholas J. Lisuzzo

RECOMMENDED:

Advisory Committee Chair

Assistant Chair, Department of Biology and Wildlife

APPROVED:

Dean, College of Natural Science and Mathematics

Dean of the Graduate School

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A

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Nicholas J. Lisuzzo, B.S.

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ABSTRACT

Accumulation of nitrogen in the early successional vegetation on the Tanana River floodplain cannot be explained by conventional measurements of soil nitrogen dynamics. This study examined these riparian areas and the effect on nitrogen cycling created by interactions among the aquatic, terrestrial, and atmospheric environments. Two hypotheses were tested; one centered on hydrologic, and one on atmospheric, mechanisms of nitrogen supply. We experimentally tested contributions of nitrogen from the hyporheic zone by measuring nitrogen-flux in the presence and absence of moving water. We then characterized hydrologic properties and ground-water chemistry along three ground-water well transects. In addition, we conducted a study to determine ambient levels of ammonia gas in the local atmosphere and to identify plants potentially utilizing atmospheric nitrogen based on stable isotope natural abundances. Static acid traps were used to calculate atmospheric levels of ammonia and mean levels ranged as high as 14 $\mu g \cdot m^{-3}$, and there was isotopic evidence that the *Salix alaxensis* communities are utilizing atmospheric ammonia. Both hydrologic and atmospheric sources of nitrogen potentially provide greater amounts of nitrogen when compared to the *in-situ* processes of nitrogen fixation, nitrogen mineralization, and nitrogen deposition during this critical transition from bare silt to productive floodplain forests.

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I. INTRODUCTION

Nitrogen is a key nutrient required for plant growth, and often is the single factor that most limits plant productivity. In interior Alaska, primary successional ecosystems along the Tanana River are initiated when bare mineral soil is exposed in silt and gravel bars that are then rapidly colonized by vegetation. During the first decade after pioneer species become established, nutrient availability is generally low, and, in particular, nitrogen inputs are extremely small. Despite this, these ecosystems are dominated by productive willow (*Salix spp.*) communities. The impetus for this research was to identify the sources and quantify the fluxes of nitrogen to these early-successional willow communities.

The study sites were located within the Bonanza Creek Long Term Ecological Research Site, located along the Tanana River downriver from Fairbanks, Alaska. The first stage of the investigation involved "data mining" the wealth of information from previous studies pertaining to nitrogen dynamics on the floodplain. At least five studies examined nitrogen mineralization, and at least four studies examined nitrogen fixation at various points in the successional sequence. Rates of nitrogen deposition for the general area have been monitored as part of the National Atmospheric Deposition Program (NADP). The closest NADP site was located at Poker Creek, approximately 100 km northeast of the study area. Data from these previous investigations and the NADP were used in concert with estimates of net primary productivity, and plant tissue nitrogen concentrations to formulate annual nitrogen budgets for four stages of succession (Table 1). Based on these budgets, a clear trend emerges with the nitrogen

requirements for the observed productivity of willow communities outstripping nitrogen supply measured as inputs from nitrogen-fixation, nitrogen mineralization and nitrogen deposition (Walker & Chapin 1986, Klingensmith & Van Cleve 1993b, Van Cleve et al. 1993a, Viereck et al. 1993a, Ruess et al. 1996, Uliassi & Ruess 2002, National Atmospheric Deposition Program 2002-2004, Ruess et al 2004). The apparent discrepancy between nitrogen supply and nitrogen demand for the willows begs the question: Prior to the establishment of the nitrogen fixing alder (*Alnus tenuifolia*), what is the source of nitrogen to these willow communities?

We proposed two hypotheses proposed addressing the discrepancy and suggesting alternate sources of nitrogen supply. The first focused around the inherently dynamic hydrologic characteristics of the sites. Because of the underlying saturated soils of the hyporheic zone, the high rates of potential evapotranspiration, and small amounts of precipitation, capillary rise is an important hydrologic process in these ecosystems. The Tanana River floodplain is characterized by the presence of a salt crust, formed by solutes transported from the hyporheic zone to the surface by capillary rise. Any nitrogen dissolved in hyporheic water would thus be transported toward the surface as water moved vertically. In addition, the water table fluctuates with changes in inputs from glacial melt waters throughout the summer, typically leading to saturation of the rooting zone for several weeks. During this period of saturation, nitrogen in subsurface water can be transported to the roots by advective flow. Although nitrogen concentration in hyporheic waters is relatively small, the net flux is potentially large enough to supply substantial amounts of nitrogen to the plants.

The second hypothesis focuses on interactions between adjacent terrestrial ecosystems. On the Tanana River floodplain, willow communities are replaced later in succession by thin-leaf alder. Soil nitrogen concentration increases dramatically under alder, whereas high soil pH (7.0 to 8.0) persists; the combination of these two factors creates an environment suited for ammonia volatilization. Alder stands may be chronically losing nitrogen via volatilization, and could supply the adjacent, nitrogen limited willow communities with gaseous nitrogen. In a similar manner to nitrogen inputs from alder stands, the heavy use of these ecosystems by moose (*Alces alces*), hares (*Lepus americanus*) and a variety of other animals could supply large amounts of nitrogen rich waste in the form of feces, urine and carcasses that then could volatilize and supply nitrogen to the vegetation.

The investigation was an integrated approach using existing data on the traditional controls of terrestrial nitrogen cycling, while testing and incorporating alternative sources of nitrogen supply to balance the nitrogen budgets for these ecosystems (Figure 1). The first chapter of this thesis tests the hypothesis that hydrologic processes contribute most of the nitrogen to the willow communities via capillary rise and sub-surface advective flow, and is formatted for submission to Ecoscience. The second chapter focuses on identifying the concentration of atmospheric ammonia and evaluating the evidence as to what extent plant communities may be using gaseous nitrogen and is formatted for submission to Oecologia.

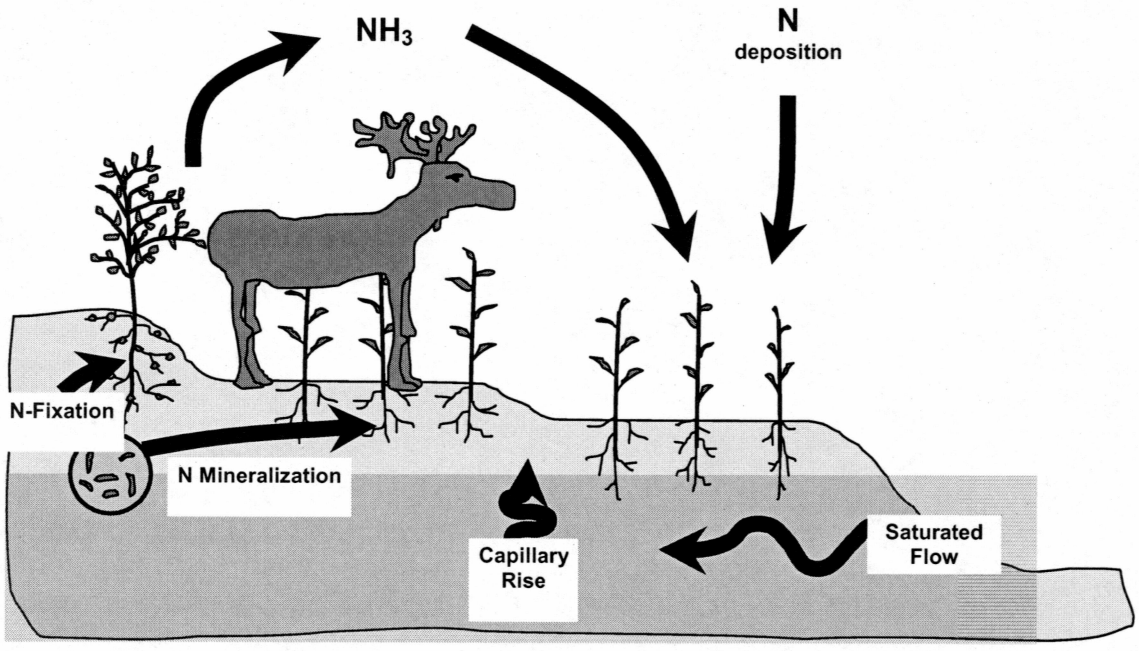

Figure 1. A conceptual model of nitrogen supply for early succession stands along the Tanana River floodplain. Traditionally measured processes of nitrogen fixation, nitrogen mineralization, and nitrogen deposition provide important contributions to seasonal nitrogen supply. In addition, capillary rise transports solutes to the rooting zone in unsaturated soils, while mass-flow supplies nutrients laterally during high water. Adjacent stands of nitrogen fixers and animal wastes volatilize nitrogen and supply developing willows with nitrogen in the form of atmospheric ammonia.

Table 1. Patterns of nitrogen supply and requirements across four stages of primary succession. All data are presented as $g \cdot m^{-2} \cdot y\text{-}1$. Constructed using data from [1] Van Cleve et al. 1993, [2] National Atmospheric Deposition Program data 2002, 2003 & 2004, [3] Klingensmith and Van Cleve 1993, [4] Uliassi and Ruess 2002, [5] Ruess et al. 1996, [6] Walker and Chapin 1986, [7] Viereck et al. 1993 and [8] Ruess et al. 2004.

Total Measured Nitrogen Inputs

Stage	Nitrogen Mineralization[1]	Nitrogen Deposition[2]	Nitrogen Fixation[3,4,5]	Total N Input
III-Willow	0.25	0.08	0.10	0.43
V-Alder	1.50	0.08	6.72	8.30
VI-Poplar	1.60	0.08	2.20	3.88
VIII-White Spruce	1.00	0.08	0.15	1.23

Annual Plant Nitrogen Requirements

Stage	Aboveground N Requirements[6,7]	Belowground N Requirements[6,8]	Total N Requirements	% N Requirement Supplied
III-Willow	1.12	0.51	1.63	26
V-Alder	4.34	2.05	6.39	130
VI-Poplar	1.78	3.04	4.82	81
VIII-White Spruce	1.47	1.63	3.10	40

II. Hydrologic controls on nitrogen availability in a high-latitude, semi-arid floodplain[1].

Abstract

Past research shows a discrepancy between nitrogen availability and the annual growth requirements for early successional plant communities along the Tanana River floodplain in interior Alaska, and can only explain approximately 26% of observed productivity. This study examined the potential for subsurface hydrology to supply nitrogen to the rooting zones of early successional plant communities throughout the growing season. Three transects of ground-water wells were established along the floodplain, and hydrologic characteristics and chemistry were monitored for two years. Hydrologic measurements were then used to model the potential nitrogen contributions from advective flow and capillary rise. Ion exchange membranes and stable isotope tracers were used to identify the use of hyporheic nitrogen by vegetation. Nitrogen accumulation on ion exchange membranes showed a large input of nitrogen during a period of high water in 2003. Plants showed uptake of hyporheic ^{15}N labeled nitrogen at two of four locations. Models of capillary rise and advective flow estimated that nitrogen supply from subsurface water accounted for additional inputs equal to 20-50% of these plant communities annual nitrogen requirements. These data suggest that hyporheic water is an important source of nitrogen for these riparian communities, and potentially explains the discrepancy between nitrogen supply and demand.

[1]To be submitted to Ecoscience as: Lisuzzo NJ, Jones JB, and Kielland K, 2005. Hydrologic controls on nitrogen availability in a high-latitude, semi-arid floodplain.

Keywords: Nitrogen, Tanana, Hyporheic, Advective flow, Capillary-rise, Riparian

Nomenclature: Hulten, 1968.

Introduction

Arctic and sub-arctic ecosystem productivity is often limited by nitrogen availability (Shaver & Chapin 1995, Atkin 1996, Ruess et al. 1996). The supply of inorganic nitrogen resulting from soil microbial processes has been a primary focus of research in the arctic tundra and the boreal forest for decades. The conventional concept of terrestrial nitrogen cycling, in the absence of nitrogen-fixers, has focused on mineralization of soil organic matter to supply plant nitrogen requirements (Vitousek & Howarth 1991, Aerts & Chapin 2002). One re-occurring theme has been the inability of nitrogen mineralization measurements to explain nitrogen accumulation in vegetation (Shaver et al. 1991, Ruess et al. 1996). In the recent years, an increasing body of evidence supports the direct uptake of organic forms of nitrogen by plants in these environments (Chapin et al 1993, Kielland 1994, Persson & Nasholm 2001, McFarland et al. 2002). Because organic nitrogen can be found in much greater concentrations than inorganic nitrogen in most high latitude soils (e.g. Kielland 1995), vegetation nitrogen demand may likely be met by organic forms.

The Tanana River floodplain is a large landscape feature, and hosts some of the most productive ecosystems in interior Alaska. A primary successional sequence

develops across the floodplain, and the earliest stages are characterized by the presence of rapidly growing willow (*Salix spp.*) communities (Van Cleve et al 1993a, Viereck et al 1993a). These communities are highly productive in spite of heavy browsing by vertebrate herbivores (McAvinchey 1991, Kielland et al 1997), repeated inundation from floods, and intrinsically low nutrient availability (Van Cleve et al. 1993b). As in other sub-arctic terrestrial ecosystems, inorganic nitrogen availability is extremely low; however, in contrast to other sub-arctic ecosystems, organic nitrogen uptake by plants likely does not play a large role in these environments. One characteristic of primary successional soils is the initial absence of a forest floor in the earliest stages. It follows that early in primary succession there would be both low rates of nitrogen mineralization (Van Cleve et al. 1993a, Klingensmith & Van Cleve 1993a), and a lack of the accumulated organic materials that characterize later successional hardwood and coniferous floodplain stands (Viereck et al 1993a). Logic dictates that in early successional communities that lack large pools of organic matter, one of two situations must occur: either established methods of measuring terrestrial inorganic and organic nitrogen supply must closely approach estimates of plant uptake, or alternate sources of nitrogen must be available.

The Bonanza Creek Long Term Ecological Research Site (LTER) encompasses a portion of the Tanana River. Previous research within the LTER shows that the earliest stages of succession follow the general regional trend where plant nitrogen requirements appear to outstrip the supply of nitrogen provided by mineralization,

fixation, and deposition. Estimates suggest that these pathways of plant nitrogen supply can account for only 26% of the nitrogen annually accrued by vegetation in these early-successional stands (Table 1; Walker & Chapin 1986, Klingensmith & Van Cleve 1993b, Van Cleve et al. 1993a, Viereck et al. 1993a, Ruess et al. 1996, Uliassi & Ruess 2002, National Atmospheric Deposition Program 2002-2004, Ruess et al 2004). The discrepancy between plant nitrogen demand and soil nitrogen supply prior to the establishment of the nitrogen fixers (i.e., thin-leaf alder *Alnus tenuifolia*) is not unique to primary succession occurring along the Tanana River, but has been observed in variety of riparian ecosystems (Adair & Binkley 2002, Anderson et al. 2003). Several mechanisms have been suggested to account for these unexplained inputs of nitrogen. For example, river water in the hyporheic zone and during floods was shown to provide both a direct and immediate input of nitrogen to riparian plant communities along Sycamore Creek in the Sonoran Desert (Shade et al. 2002). Moreover, along the Yampa and Green Rivers in Colorado the accumulation of nitrogen across two hundred years of succession has been explained by annual deposition of nitrogen in floodwater sediments as the waters recede (Adair et al 2004). Although many studies have addressed nitrogen sources in early succession, the relative importance that hydrologic nitrogen supply may play in a variety of different riparian areas is not fully understood.

The nitrogen dynamics of a plant community are controlled by the rate by which nitrogen is made available to plant roots (Barber 1962). There are three potential ways hydrologically dynamic areas can increase nitrogen supplyin comparison to other

terrestrial environments: 1) subsurface water can stimulate microbial activity by altering the soil environment (e.g., moderating temperature, providing labile carbon etc.), 2) the presence of subsurface water can increase pool size via access to otherwise unavailable sources (e.g., dissolved nitrogen in groundwater or allochthonous inputs from floods), or 3) subsurface water can accelerate the rate of supply by flowing through the rooting zone. In previous studies of nitrogen dynamics along the Tanana River, inputs from subsurface water were not accounted for because mineralization studies have used water impermeable containers (i.e. polyethylene bags, PVC tubes etc.) that prevent leaching, but exclude any inputs of hydrologically transported nitrogen. If water is moving at rates that substantially exceed the rate of diffusion, then a small pool of dissolved nitrogen could equate to a significant supply for plant uptake. Another distinctive feature of the soils on the Tanana floodplain is the presence of a salt crust. This crust is created by transportation of calcium and magnesium sulphate from the ground-water to the surface by evapotranspiration, and this process of capillary rise likely transports dissolved nitrogen with other solutes from ground-water to the surface soil (Dryness and Van Cleve 1993).

In this study the nitrogen dynamics of the early successional stage of the Tanana River floodplain were examined, taking advantage of both the location and the substantial body of existing research. The objectives of this research were threefold: (1) to identify the sources of nitrogen supply to early successional stands, (2) to quantify the relative importance of each source, and (3) to determine the controls on nitrogen

availability within this system. Two hypotheses were tested involving hyporheic fluxes as the primary mechanisms of nitrogen supply to plants on the Tanana River floodplain.

Hypothesis I: The majority of plant-available nitrogen is supplied to the root matrix throughout the growing season via vertical capillary rise.

Hypothesis II: The majority of plant-available nitrogen is supplied horizontally by saturated subsurface flow through the rooting zone during high water.

Methods

Site Description

The study was conducted at the Bonanza Creek LTER (64° 48' N, 147° 52' W) about 30 km southwest of Fairbanks, Alaska and encompassing early successional plant communities along the Tanana River floodplain. The Tanana River forms near the border of Alaska and Canada, and drains a basin with an area of 113,920 km^2 (http://www.lter.uaf.edu/). The river follows a general path to the northwest for approximately 850 km before flowing southwest, and then north into the Yukon River. Downriver from Fairbanks, the Tanana River Valley opens to 80-100 km in width, and contains an active floodplain of 300-2000 m across. At the study sites the Tanana River forms of a series of braided channels with sandbars and islands.

The frost-free growing season is approximately 100 days, and air temperature varies from -50° C to 25° C through the year. A rain shadow created by the neighboring Alaska Range results in the study area receiving 269 mm of mean annual precipitation, approximately 37% of which is snow (Viereck et al. 1993b). Potential

evapotranspiration approaches twice the amount of annual precipitation (Viereck et al. 1993b), implying ground-water and the river could act as important sources of water for biological communities along the floodplain. Floods, accompanied by the deposition of sediment, occur periodically, and aggradation as a result of river meander leads to the development of exposed alluvium. Soil particles are primarily a mix of sand and silt of glacial origin, and are classified as Cryofluvents. The soil pH of these sites is typically between 7 and 8, and is directly related to high concentrations of base cations (Dyrness and Van Cleve 1993). Among the first woody plant species to colonize are a variety of willows (*Salix interior, S. alaxensis*, *S. nova-anglea*, *S. branchycarpa*, *S. lasiandra* and others) and thin-leaf alder (*Alnus tenuifolia*). In later stages of succession, balsam poplar, white spruce and black spruce (*Populus balsamifera*, *Picea glauca*, and *P. mariana,* respectively) dominate the overstory vegetation.

Willow maintains dominance for the first decade of succession, until browsing pressure from mammalian herbivores (*Alces alces*, *Lepus americanus*, Kielland et al 1997) and diminishing soil salt content, as a result of reduced evaporation beneath the developing forest floor and repeated leaching from rain events (Chapin & Walker 1993), allow alder to colonize and assert its dominance. During stand dominance by alder, soil nitrogen pools increase rapidly and provide much of the nitrogen found in later stages of succession.

Hyporheic Measurements

At early successional sites, separated by up to 10 river km, transects of ground-water wells were established (Figure 1). Wells consisted of 4 cm PVC pipes 3 m in length, with the lower 1.5 m being perforated, and wrapped in Geotextile® cloth to prevent filling of wells with sediment. Transects ranged from 500 to 1000 m in length, and wells were installed to a depth of 2 m. Water levels in wells were measured every two weeks from early June to mid-September throughout the summers of 2003 and 2004. Soil cores were taken at 3 locations along each transect, to a depth of 120 cm, and analyzed for hydraulic conductivity in the lab using a falling head permeameter (Scott 2000). Particle size analysis was also performed on these soils using the buoycous method (Elliot el al 1999). Subsurface flow rates were provided by H. Clilverd (Bonanza Creek LTER, unpublished data).

On each sampling date, 100 mL of water from each well was collected in polyethylene bottles. Prior to collection bottles were acid washed and then triple rinsed with sample water from each well in the field. Samples were stored in a cooler and immediately returned to the lab, refrigerated and filtered within 24 hours. Samples were analyzed by ion chromatography (Dionex Corporation, Sunnyvale, CA) for nitrate and nitrite concentrations, and sub-samples were frozen and analyzed for ammonium at a later date. Total dissolved nitrogen (TDN) was determined by running sub-samples through a Shimadzu 5000 total organic carbon analyzer (Shimadzu Scientific, Kyoto, Japan) plumbed to an Antek 7050 nitrous oxide chemoluminescent detector (Antek

Instruments, Houston, TX). Dissolved organic nitrogen (DON) was calculated as TDN minus the sum of nitrate, nitrite, and ammonium in each sample.

Data from the United States Geological Survey (USGS) gauging station (#15485500), located on the Tanana River 30 km upriver in Fairbanks, AK, were used to create a relationship between river discharge ($m^3 \cdot s^{-1}$) and the depth to water measured in wells at the sites for the two study years. This relationship was then used to estimate seasonal fluctuations in the water table over the past three decades using archived river discharge data. This allowed the hydrologic regime of the two study years to be compared and placed in longer-term context, and increased our confidence that data presented are representative of a typical year. Potential evapotranspiration rates were calculated using the Thornwaite Method (Thornwaite & Mather 1955, Sellinger 1996).

Ion Exchange Membranes

Ion exchange membranes (CMI 7000 & AMI 7001, Membranes International, Glen Rock, NJ) were deployed to assess nitrogen supply at 8 points along each transect. Membranes are used to estimate inorganic nitrogen availability and are sensitive to changes in soil water conditions (Sherrod et al 2002, Langlois et al 2003, Sherrod et al 2003a, Sherrod et al. 2003b). Membranes were deployed once per month throughout the growing season in 2003, and twice per month in 2004 for 15 day incubation periods. Although ion exchange membranes can be deployed for up to one month *in-situ* (Qian & Schoenau 2002), a shorter deployment length was chosen to ensure that saturated

adsorption dynamics did not occur during the experiment as a result of the large concentration of solutes. Prior to deployment in the field, membranes were shaken in 3 % concentrated HCl for one hour. Membranes were then placed in 0.5M $Na(CO_3)_2$, shaken for one hour, the solution was then poured off, replaced and shaken for a total of three times. Following the third $Na(CO_3)_2$ treatment, membranes were briefly rinsed with de-ionized water, and stored moist until deployment the following day. At each location, two intact, replicate soil cores 10 cm in diameter and 15 cm in length were taken. Each core was cut in half vertically, and a cation and an anion exchange membrane were placed in between the halves. A paired sample design was used so that at each location there were two replicate cores receiving different treatments for each sample date. One treatment consisted of cores being reassembled and placed into a water impermeable polyethylene bag, typically used for buried bag incubations, and open to nitrogen inputs from both mineralization and free-living nitrogen fixers. The second treatment consisted of a water permeable nylon mesh bag that was open to inputs from soil microbial processes and both capillary rise and saturated subsurface flow. Both cores were then placed back into the ground. This provided a directly comparable index of *in-situ* nitrogen availability in the presence (water permeable) and absence (water impermeable) hydrologic nitrogen sources. Following incubation, membranes were extracted in 0.5M K_2SO_4 for 1 h, and analyzed with a Bran-Lubbe auto-analyzer (SPX Corporation, Delavan, WI) using the phenol-hypochlorite method

for NH_4^+ and the sodium nitroferrocyanide-cadmium reduction method for NO_3^- (Page 1982).

Nitrogen Mineralization

In the summer of 2003 standard buried bag incubations (Eno 1960, Binkley & Hart 1989) were used to measure rates of net nitrogen mineralization along each transect. The presence of buried organic horizons as a result of periodic sedimentation events provides the potential for increased nitrogen mineralization rates at depth. Buried bags were placed adjacent to ion exchange membranes at each of the 8 locations along each transect at depths of 25 and 50 cm, and incubated *in-situ* for 15 days at three dates during the summer. Initial and final soil cores were returned to the lab, passed through a 2 mm sieve, and homogenized. Sub-samples were collected and dried at 105° C to establish fresh weight to dry weight ratios. Soils were then extracted with 0.5M K_2SO_4 and were run on the auto-analyzer using the same methods used for ion exchange membranes extracts. Nitrogen mineralization measurements were discontinued in 2004.

Capillary Rise and Saturated Flow

Hyporheic nitrogen supply was calculated as a function of subsurface water flux via two mechanisms, either capillary rise under unsaturated conditions, or saturated flow through the rooting matrix under high water conditions. Separate mathematical models were applied to calculate rates of nitrogen supply for both mechanisms.

Nitrogen data from well water samples and soil-hydraulic properties were used to estimate capillary rise using the model UPFLOW (Raes and Deproost 2003, Raes 2004). UPFLOW is a mathematical model that uses soil and environmental characteristics to predict vertical solute transport based on Richard's equation for unsaturated flow. Model inputs were potential evapotranspiration ($mm \cdot d^{-1}$), mean soil water content (volume %), water table depth (m), soil horizon depth (m), soil particle size (% sand, silt, clay) and salt content of water table ($dS \cdot m^{-1}$). The resulting output consisted of the total vertical flux of water to the soil surface ($mm \cdot d^{-1}$) and total salt flux ($tons \cdot ha^{-1} \cdot year^{-1}$). Total nitrogen flux from capillary rise was then calculated by multiplying the ratio of total dissolved nitrogen to total dissolved solutes by the total salt flux. Because UPFLOW was developed for agricultural settings, no suitable vegetation class was available to represent floodplain vegetation. All estimates were therefore calculated for barren soil.

Average rooting depth was measured for the dominant species of willow (*S. interior* & *S. alaxensis*) along exposed river banks during a period of low water level for the Tanana River in August 2004. Soil porosity was calculated using bulk density measurements from Van Cleve et al. (1993b), and was corroborated by measuring a subset of the soils from hydraulic conductivity measurements in the lab. The saturated area of the rooting zone was calculated using the average rooting depth and the water level from well measurements. Subsurface flux was calculated as:

$$Q = v \cdot \Phi \cdot A \qquad [1]$$

Where Q = subsurface flux ($m^3 \cdot d^{-1}$)

v = subsurface flow rate ($m \cdot d^{-1}$)

Φ = porosity

A = Cross-sectional area of rooting zone saturated (m^2)

The rate hyporheic nitrogen flux from saturated flow was then calculated by multiplying the sub-surface flux by the nitrogen concentration measured in the ground-water wells.

Estimates for advective nitrogen flux and capillary rise based on 30-year-daily-means for water table height were calculated using mean values for hyporheic chemistry measured in this study. The growing season was divided into 7 periods, 15 or 16 days in length, to facilitate comparisons with ion exchange membrane and buried bag mineralization measurements, and fluxes were calculated using mean values pooled across sites for the input variables during each time period. The FP1C site (Figure 1) was not included in estimates of capillary rise and saturated subsurface flow due to extremely high nitrogen concentrations in the hyporheic zone found there. Although the exact reason for the high concentrations of nitrogen was not investigated, it was assumed to be a result of the presence of large numbers of thin-leaf alder along sections of this transect.

Plant Use of Hyporheic Nitrogen

To evaluate the importance of plant uptake of hyporheic-derived N, stable isotopes were used to track nitrogen flow from the hyporheic zone to the vegetation. At two of the study sites (FP1B, and Deborah's Island), two hollow flow-boxes were installed within the general vicinity of the well transects. Each flowbox was constructed of perforated PVC sheets 3 m long, 0.4 m tall and 0.04 m thick, and had an internal volume of approximately 30L. The flow-boxes where installed to a depth of 1.3 m, with the top buried below the rooting zone. Hyporheic water within each box was labeled by adding 500 mL of a solution containing 9.0 mM $^{15}NH_4Cl$ and 5.0 mM $K^{15}NO_3$ (99% atom, Icon Isotopes, Summit, N.J.) to two flow-boxes (Deborah's Island) on July 1st, 2004 and to two flow-boxes (FP1B) on July 13th, 2004. The labeled solution was circulated with hyporheic water in each flow-box using a peristaltic pump for two hours to ensure uniform mixing. At the time of sets of both injections the water was approximately 10 cm below the top of the flowboxes, and thus 20 – 30 cm below the mean rooting depth. The area "downriver" from the injection point was divided into sections 1 m long and 3 m wide for 10 m. Every seven days after the addition, six soil cores 3 cm in diameter were collected to depths of 30, 60 and 90 cm from each section and composited by depth. After three weeks (July) or four weeks (August) shoot and leaf tissues in the form of one randomly selected intact branch with foliage from each plant were collected in addition to the soil samples. Six cores 10 cm in diameter and 25 cm long were also taken on the last sampling date from each section. The roots were

sampled from these cores *in situ* by washing cores through a 0.5 mm sieve using river water. As willows were the only woody species in these sampling areas, their larger roots could be identified. Non-woody roots greater then 1 mm in diameter were removed and discarded; roots smaller then 1 mm in diameter could not be reliably sorted, and were left in the sample. Control samples were collected 2 m upriver from the injection point on the same sampling schedule. Plant tissues (leaf, root, and shoot) and soils were dried at 65° C for 48 hours. All samples were ground in a ball mall, or using a Wiggle-bug® and analyzed for $\delta^{15}N$ using a continuous flow mass spectrometer (PDZ Europa Inc., Cheshire, UK).

Statistics

Statistical analyses were performed using Statistix 8 (Analytical Software, Tallahassee, FL). Significant differences in ion exchange membrane nitrogen accumulation for the various treatments and incubation dates were tested using two-way Analysis of Variance (ANOVA); where significant differences were found Tukey's Multiple Comparisons tests were also performed.

Results

Annual Variation in Fluvial Dynamics

Surface soils ranged from being dry and cracked to being completely saturated both years. Water levels measured along all three transects varied by more than 1.5 m throughout both summers. A strong, logarithmic correlation was found between water level and river discharge (Figure 2).

The seasonal variation in discharge over the last 30 years indicates that discharge typically increases through out the summer, peaking in early August and declining into September (Figure 3). During the two study years the sites experienced different seasonal patterns in discharge. Discharge in 2003 was variable in mid to late summer, twice exceeding 2,300 $m^3 \cdot s^{-1}$ that resulted in floods that submerged the sites in up to 1 m of water. These floods occurred following storm events, and coincided with the peak flow of glacial melt of the Alaska Range in mid-summer. During this period, approximately 1 - 4 cm of sediment was deposited on the study sites. In contrast, 2004 was characterized by relatively high discharge throughout the summer from late May until mid-August. Although surface soils approached saturation during mid-June, no flooding occurred. A summary of soil and hyporheic properties is presented in Table 2.

Ion Exchange Membranes

In the summer of 2003 ion exchange membranes showed differences in total nitrogen accumulation both by location and by incubation date (Table 3). There was

also a marginally significant increase in nitrogen accumulation to the water permeable treatment compared to the water impermeable treatment. Patterns in total nitrogen accumulation were largely driven by an approximately 400% increase in nitrogen supply during the incubation period that began between the two floods that occurred in July (Figure 4).

In the summer of 2004 ion exchange membranes showed a difference in total nitrogen accumulation only by date (Table 3). There was no difference in nitrogen supply between the water permeable and water impermeable treatments, or between locations along the transects. Higher rates of accumulation were observed early in June and at the end of the summer in September 2004 (Figure 4). Accumulation rates for most of the growing season were similar to those found during 2003 with the exception of during the floods.

Nitrogen Mineralization

Nitrogen mineralization rate throughout the summer of 2003 was low (Figure 5) and did not vary significantly with depth (ANOVA, $\alpha = 0.05$, $n = 106$).

Capillary Rise & Saturated Flow

Based on the model output capillary rise was predicted to occur during every incubation period for both years of the study (Figure 6). In the summer of 2003 capillary rise was extremely low until the mid-summer storms. Following the periods

of high rainfall capillary rise became comparable to both the 2004 growing season and the 30-year average. The total flux of nitrogen for 2004 and the 30-year average was fairly consistent throughout the growing season. Seasonal totals of nitrogen flux from capillary rise were between 3 and 6% of the annual nitrogen requirements for the willow communities (Table 1, Figure 6).

Saturated subsurface flow occurred in the rooting zone during a four week period in 2003, and an eight week period in 2004 (Figure 7). Model predictions based on the 30-year mean showed subsurface flow occurring in the rooting zone for 11 weeks of the summer. The supply of nitrogen to the rooting zone was approximately 20-50% of the annual nitrogen requirements for the willow communities (Table 1, Figure 7).

Plant Use of Hyporheic Nitrogen

Uptake of hyporheic ^{15}N was observed in foliage and stem tissue at 2 of the 4 flow-box locations in 2004 (Figure 8), with enrichment in foliar $\delta^{15}N$ values of approximately 7 and 10 ‰ at flow-boxes located at the upriver ends of FP1B and Deborah's Island respectively; the other two flow-box sites showed no sign of isotopic enrichment. Soil and root tissue showed no signs of the tracer at any of the sites.

Discussion

Riparian Soil Nitrogen Dynamics

Riparian ecosystems have nitrogen cycles that operate under additional controls compared to many other terrestrial ecosystems, and traditional methods for quantifying soil nitrogen availability fail to explain rates of accumulation in vegetation (Adair & Binkley 2002, Anderson et al 2003). Subsurface hydrology exerts strong controls over biogeochemical processes in riparian ecosystems, but previously has not been adequately quantified along the Tanana River. Recent studies in other riparian areas have focused more attention on fluvial processes, primarily in regard to changes in the soil environment following floods, and changes in rates of microbial processes associated with inundation magnitude and duration (Anderson et al 2003, Anderson & Nelson 2003, Sabater et al 2003). For example nitrogen accumulation for the Yampa and Green Rivers in north-western Colorado was recently attributed to nutrients stored in the sediments deposited during floods (Adair et al. 2004). Although total accumulation of soil nitrogen over succession may be explained by sedimentation in some ecosystems, this process likely does not explain the discrepancy observed in early succession along the Tanana. Sedimentation is sporadic, occurring only in years with very high water levels. Recent research has shown that both rates of decomposition and nitrogen mineralization decrease exponentially as rates sedimentation increase (Lockaby et al. 2005). Finally, if 80% of soil nitrogen in the semi-arid riparian zone is ecologically "stable", i.e. not available for uptake, then the floodplain soils only contain

enough nitrogen for a single year of growth throughout the first decade of succession (Kaye et al. 2003). This suggests that alluvial stores of nitrogen alone would not explain the discrepancies between rates of nitrogen supply and plant nitrogen uptake in the Tanana River's flooplain willow communities.

Hyporheic Control of Nitrogen Flux

Riparian ecosystems have long been recognized as a having important influences on nitrogen cycling as a result of interactions between the terrestrial and aquatic environments. Changes in water table depth can directly control soil microbial processes, with the dominant mechanism of nitrogen transformation shifting between net nitrogen mineralization, nitrification, and denitrification with fluctuations in the water table of less than 0.5 m (Hefting et al. 2004). Nitrate removal as a result of plant uptake and denitrification is also typical of riparian areas (Peterjohn & Correll1984, Schade et al. 2001, Sabater et al. 2003). In particular, floods have been suggested as a mechanism for increases in nitrogen supply via deposition of organic matter with sediment or direct supply from floodwater (Shade et al. 2002, Adair et al 2004).

The data in this study suggest that a significant amount of nitrogen could be supplied directly from flowing water. The greatest flux of nitrogen from subsurface flow in the rooting zone coincided with the ion exchange membrane deployment that accumulated the greatest amount of nitrogen throughout the summer of 2003. During this period of high subsurface flux the membranes accumulated nitrogen at rates

comparable to membranes in stands of *Lupinus spp.* in Sweden (Myrold & Huss-Danell 2003). These stands of *Lupinus* had mean rates of nitrogen mineralization over an order of magnitude greater (18 times) than the highest rates of mineralization recorded for the Tanana willow communities (Van Cleve et al. 1993a). Other than during the flood of 2003, rates of accumulation were in the lower range of values reported from literature for ecosystems without nitrogen-fixers (Huang & Schoenau 1997, Hang et al. 2004). Ion exchange membrane data from 2004 did not show the same connection to predictions of advective flow, potentially due to the fact that ion exchange membranes were buried at 25 cm, while advective flow predictions were based on a 75 cm deep rooting zone. Most of the nitrogen supplied to these ecosystems from hydrologic processes was predicted to occur during periods of high water that would not typically be considered floods, and at depths greater than the top 25 cm of mineral soil often used in nitrogen cycling studies.

Stable isotope enrichment demonstrated that willows assimilated hyporheic nitrogen at times during the growing season. Although the relative importance of hyporheic supply to annual nitrogen budgets was difficult to assess based on the isotope data, a recent study using a similar technique estimated plant uptake of 1 $gN \cdot m^{-2}$ over a 40 day period in a semi-arid floodplain located in the Sonoran desert (Shade et al. 2005). The uptake of ^{15}N at some sites in this study, but not at other sites along the Tanana River, suggests that a spatial threshold exists that dictates the availability of hyporheic nitrogen to plants. Both water level and micro-topography appear to interact

to create a zone where hyporheic water must flow before fine root density is high enough for plants to access significant amounts of nitrogen. Regardless, the data in this study show that, not only are there large fluxes of hyporheic nitrogen to the rooting zone along the Tanana River's riparian zone, but that the dominant plant communities are capable of readily assimilating that nitrogen. Establishing nitrogen absorption dynamics for roots at different depths in the soil profile may be critical to improving our understanding of the thresholds that regulate how and when plants can use substantial hyporheic fluxes of nutrients.

Alternate Sources of Nitrogen

Large inter-annual variation in water level makes it difficult to assess exactly how much nitrogen is supplied from the hyporheic zone. Microbial processes coupled with hydrologic supply of nitrogen still may not account for all nitrogen uptake by plants at these sites, suggesting that there are still could be unaccounted sources of nitrogen. Sediment and litter deposited during years when substantial flooding occurs, undoubtedly supply nitrogen for mineralization by microbial communities. The alkalinity of these soils also presents another possible nitrogen source in the form of stomatal uptake of atmospheric nitrogen gas. The combination of large pools of soil nitrogen and high pH could create significant fluxes of volatilized ammonia under stands of thin-leaf alder that dominate mid succession (Sharpe and Harper 1995). This

gaseous nitrogen could potentially be carried by local air currents and absorbed via the stomata of nitrogen-limited willow communities (Hutchinson 1972).

Finally, the period of saturated flow in the rooting zone calculated in this study may represent only a portion of the growing season when water is flowing through the rooting zone. In late spring, surface soils are saturated with flowing water resulting from snowmelt. Freeze-thaw cycles and snowmelt are known to release and transport large amounts of nitrogen. For example, at Hubbard Brook Experimental Forest, 69% of annual stream export of nitrate occurs during snowmelt (Likens and Bormann, 1995) and freeze-thaw events were found to result in as much as a 400% increase in DON export (Fitzhugh et al. 2001). The tail-end of seasonal snowmelt may coincide with the period when plant requirements of nitrogen are large.

Conclusion

Saturated flow in the rooting zone and capillary rise supply between an estimated 0.35 and 0.91 $gN \cdot m^{-2} \cdot y^{-1}$ to the rooting zone in early successional stands of the Tanana River floodplain. Previously measured inputs from nitrogen mineralization and fixation studies, equaling approximately 0.43 $gN \cdot m^{-2} \cdot y^{-1}$, combined with hydrologic inputs can explain between 50 and 80% of annual nitrogen requirements. Although hydrologic nitrogen supply displayed large inter-annual variation, these hyporheic fluxes likely represent one of the major mechanisms of nitrogen supply in this ecosystem, equaling or exceeding rates of nitrogen mineralization. Incorporating

periodic sedimentation, nutrient fluxes following snow melt, and potential contributions from over-winter nitrogen mineralization, the majority of these willow communities' nitrogen requirement is likely met. These hydrologic processes appear critical to the transition from bare silt to forests not just by regulating water supply and the physical structure of the environment, but also by supplying a vital source of nutrients to these nitrogen limited systems.

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Table 1. Patterns of nitrogen accumulation across four stages of primary succession. All data are presented as $g \cdot m^{-2} \cdot y\text{-}1$. Constructed using data from [1] Van Cleve et al. 1993, [2] National Atmospheric Deposition Program data 2002, 2003 & 2004, [3] Klingensmith and Van Cleve 1993, [4] Uliassi and Ruess 2002, [5] Ruess et al. 1996, [6] Walker and Chapin 1986, [7] Viereck et al. 1993 and [8] Ruess et al. 2004.

Total Measured Nitrogen Inputs

Stage	Nitrogen Mineralization[1]	Nitrogen Deposition[2]	Nitrogen Fixation[3,4,5]	Total N Input
III-Willow	0.25	0.08	0.10	0.43
V-Alder	1.50	0.08	6.72	8.30
VI-Poplar	1.60	0.08	2.20	3.88
VIII-White Spruce	1.00	0.08	0.15	1.23

Annual Plant Nitrogen Requirements

Stage	Aboveground N Requirements[6,7]	Belowground N Requirements[6,8]	Total N Requirements	% N Requirement Supplied
III-Willow	1.12	0.51	1.63	26
V-Alder	4.34	2.05	6.39	130
VI-Poplar	1.78	3.04	4.82	81
VIII-White Spruce	1.47	1.63	3.10	40

Table 2. Two-way ANOVA results for the total nitrogen accumulation on ion exchange membranes. Data represents 15 d deployment periods as measured by membranes for the a) 2003 and b) 2004 growing seasons.

	Variable	df	MSE	*F*	*P*
a) 2003	Treatment	1	1.21	3.15	0.07
	Deployment Date	2	11.49	29.99	<0.001
	Location	24	0.6	1.57	0.05
	Error	192			
b) 2004	Treatment	1	0.19	0.64	0.43
	Deployment Date	6	3.69	12.71	<0.001
	Location	13	0.19	0.66	0.8
	Error	218			

Table 3. Summary of soil and hyporheic properties along the early successional stands of the Tanana River. Hydraulic conductivity, velocity and nitrogen concentrations are means ± **SE**.

Transect Location	% Sand	Hydraulic Conductivity ($m\ d^{-1}$)	Velocity of Hyporhiec Water ($m\ d^{-1}$)	Concentration of Nitrogen in Hyporhiec Water ($\mu g\ L^{-1}$)	Ratio of Organic to Inorganic Nitrogen in Hyporhiec Water
FP1B	59	9.2 ± 3.4	0.39 ± 0.06	148.8 ± 16.1	2.0
FP1C	60	25.0 ± 6.2	N/A	743.5 ± 113.6	5.8
Deborah's Island	69	14.0 ± 3.7	0.37 ± 0.07	181.1 ± 13.1	5.9

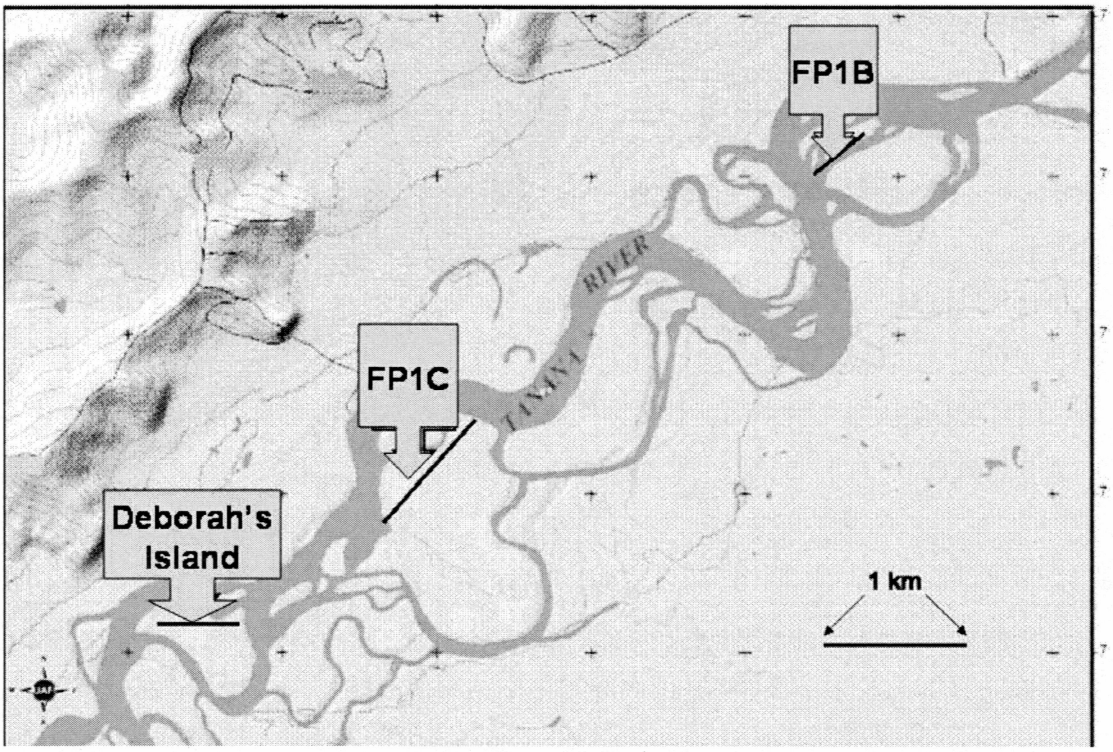

Figure 1. Location of ground-water well transects along the Tanana River floodplain.

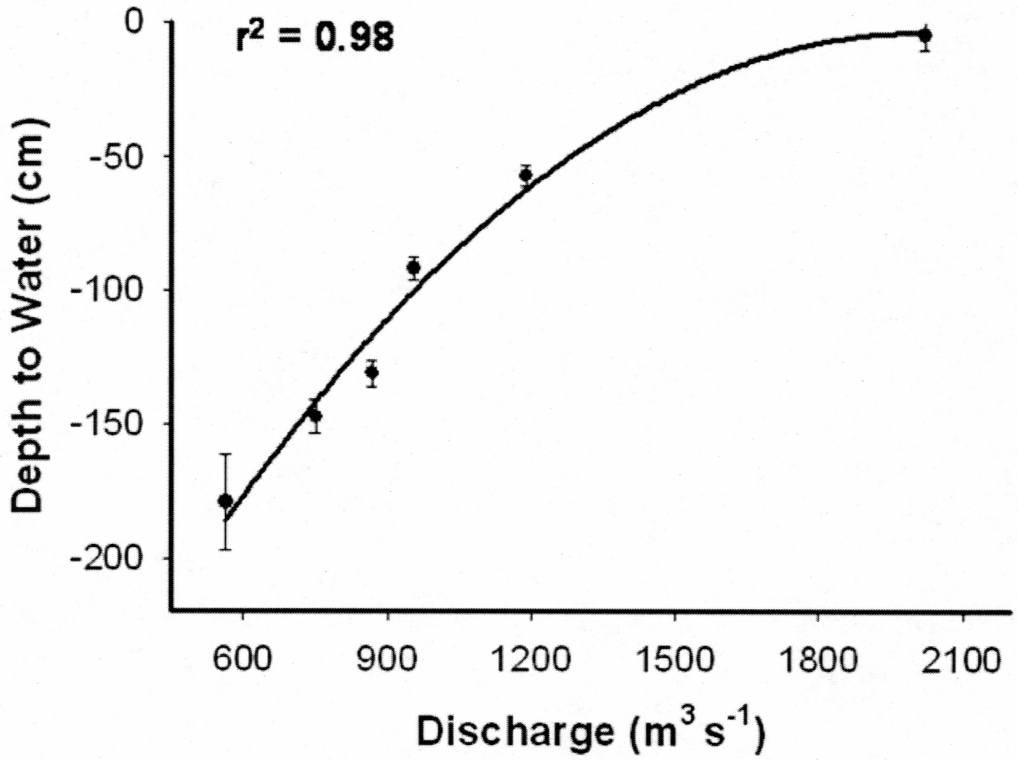

Figure 2. The relationship between river discharge for the Tanana River and waterlevel. Discharge was measured at the Fairbanks gaging station (USGS #15485500) and depth to water was measured in sample wells. Means for the 2003 growing season ± **SE**.

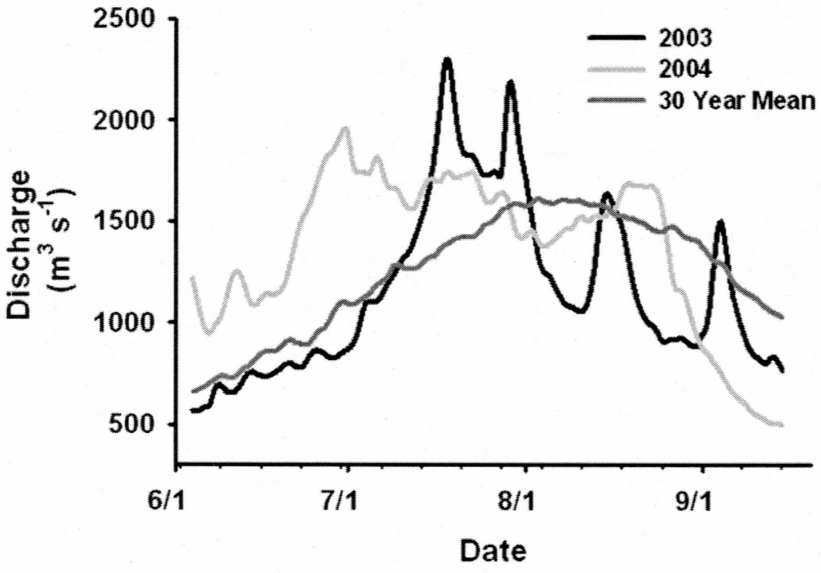

Figure 3. Seasonal fluctuations in discharge. Mean daily discharge for the Tanana River for the 2003 and 2004 growing seasons and the average calculated for the period from 1971 to 2001.

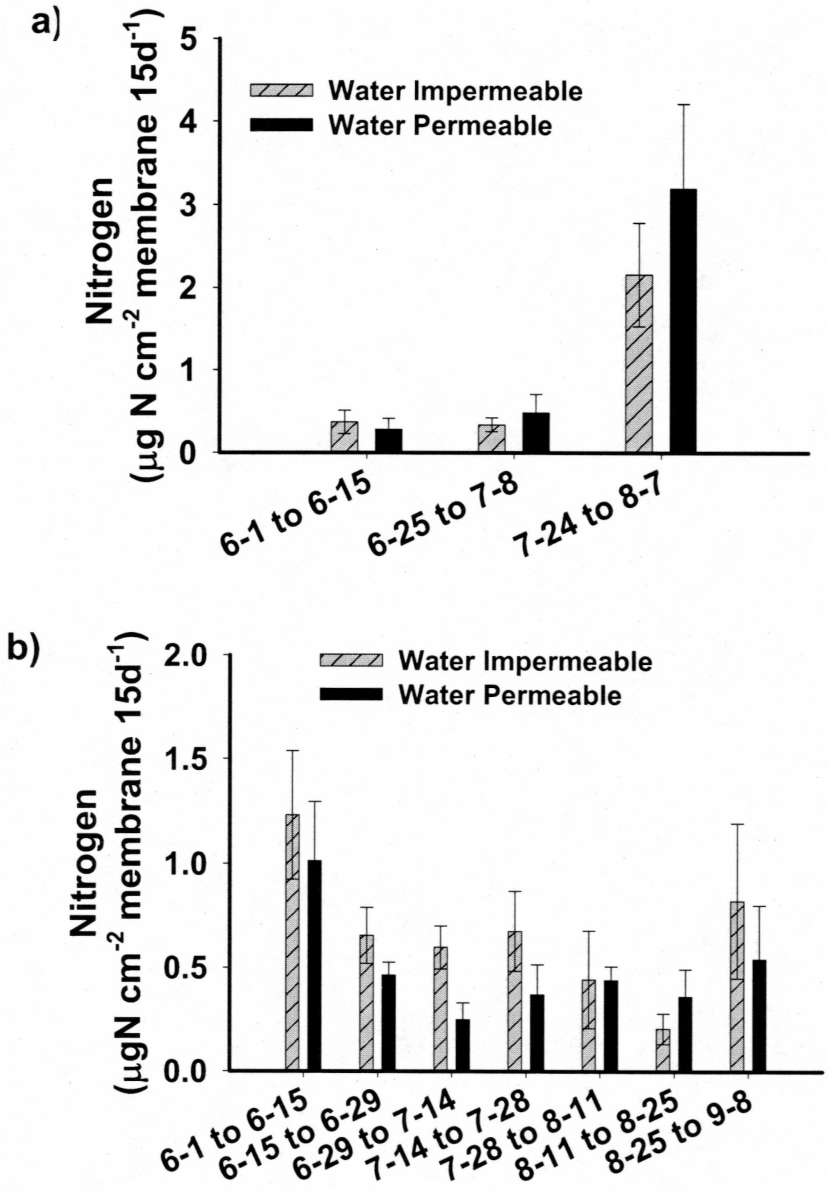

Figure 4. Seasonal variation in total nitrogen accumulated on ion exchange membranes. Calculated over 15 day incubations during a) the 2003 and b) the 2004 growing seasons. Data presented for both water impermeable and permeable treatments as means ± **SE**.

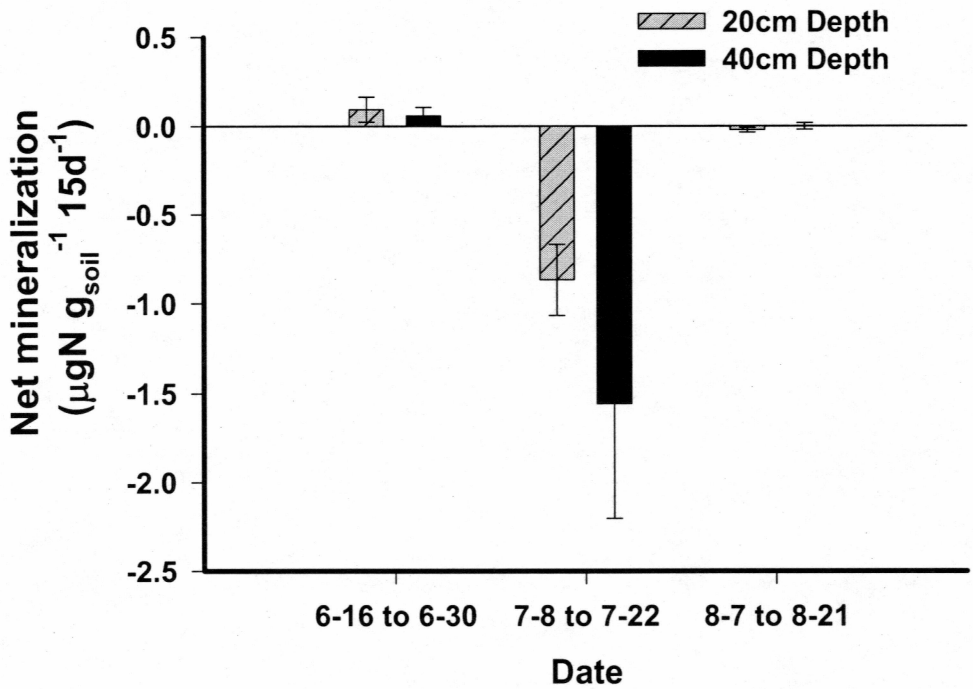

Figure 5. Net nitrogen mineralization rates for the 2003 growing season. Data are means ± **SE**.

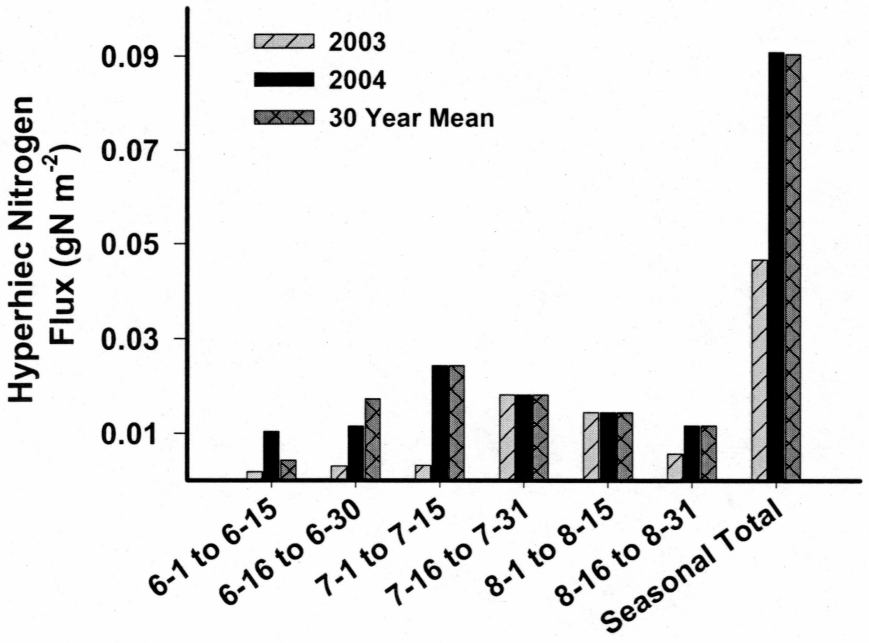

Figure 6. Predicted supply of nitrogen from capillary rise. Presented as total dissolved nitrogen transported to the rooting zone over periods of 15 days. Data are means for 2003, 2004 and estimates based on the 30 year daily mean river discharge.

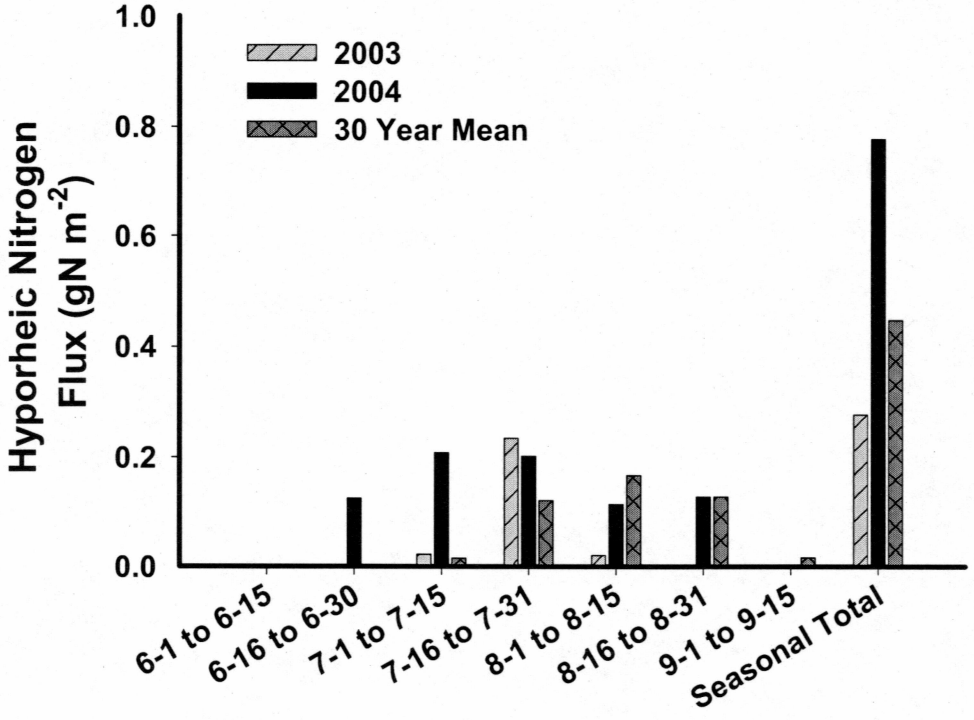

Figure 7. Predicted supply of nitrogen from saturated flow. Presented as total dissolved nitrogen transported to the rooting zone over periods of 15 days. Data are means for 2003, 2004 and estimates based on the 30 year daily mean river discharge.

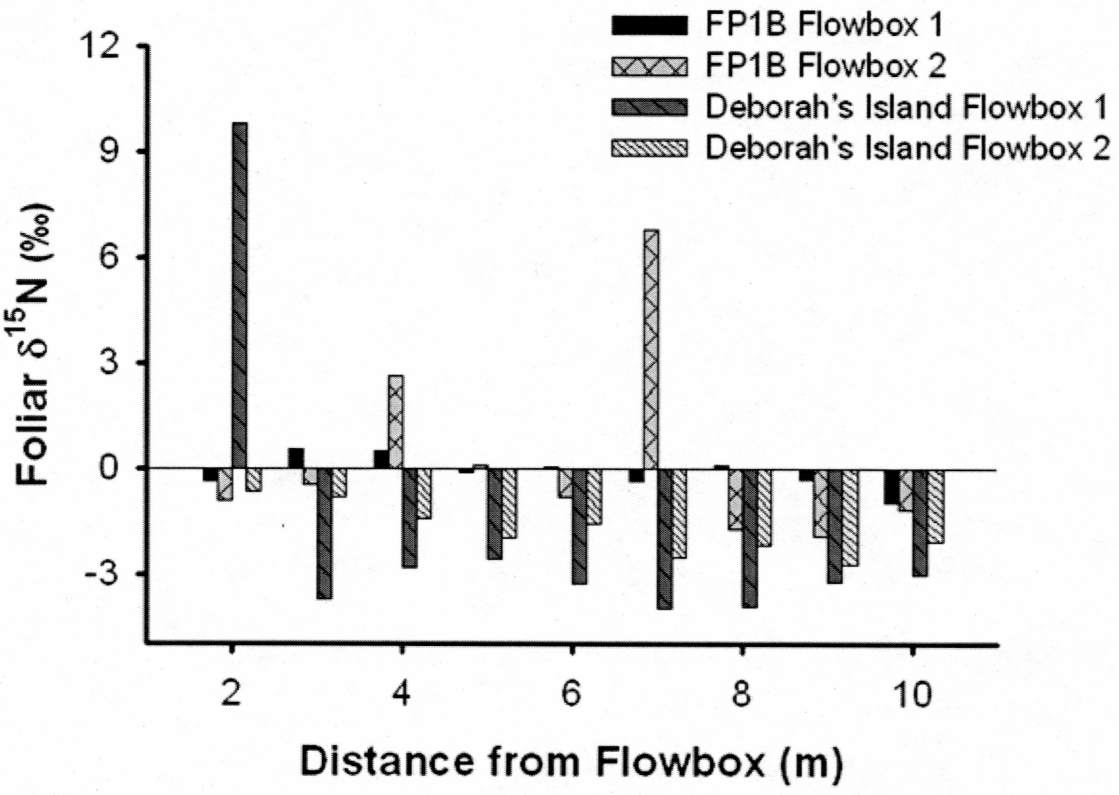

Figure 8. Plant use of hyporheic nitrogen. Isotopic signature of willow foliage 4 weeks (FP1B) and 3 weeks (Deborah's Island) after injection of ^{15}N labeled nitrogen into ground-water at a depth of 1.3 m.

III. Soil-Atmosphere-Plant interactions alter nitrogen availability during primary succession in floodplain ecosystems[1].

Abstract

Rapid accumulation of nitrogen in the vegetation of early successional stands along the Tanana River cannot be explained by nitrogen availability as measured by the contributions from nitrogen mineralization, fixation, and deposition. A hypothesis that plants were absorbing substantial amounts of ammonia gas via stomata was tested. Ammonia concentration was measured using static acid traps in five different ecosystems representing the primary successional sequence found along the floodplain. natural abundance of $\delta^{15}N$ was used to identify areas of soil enriched by the fractionation associated with ammonia volatilization, and to identify plants incorporating the resulting depleted ammonia gas into the tissue of their foliage. There was a strong relationship between total soil nitrogen, foliar nitrogen concentrations, and foliar $\delta^{15}N$ for one of the dominant species, *Salix alaxensis*, indicating a dependence on depleted ammonia in low-nitrogen environments. A negative relationship was also found between foliar $\delta^{15}N$ and proximity to nitrogen-fixing alder which is consistent with the hypothesis of nitrogen volatilization and absorption. This relatively unstudied source of nitrogen could play a critical role in controlling the productivity of semi-arid riparian zones during the transition from bare alluvium to a developed forest soil.

[1]To be submitted to Oceologia as: Lisuzzo NJ and Kielland K, 2005. Soil-Atmosphere-Plant interactions alter nitrogen availability during primary succession in floodplain ecosystems.

Introduction

Nitrogen is the nutrient that most often limits terrestrial plant growth in non-tropical ecosystems and, as such, is important to the fundamental understanding of ecosystem level processes (Vitousek 1982, Shaver & Chapin 1995, Aerts & Chapin 2002). Although nitrogen composed most of the Earth's atmosphere, it exists primarily in a form that is unavailable for absorption by plants until reduced by nitrogen fixation. The limited contributions of nitrogen-fixers to pools of plant-available nitrogen in temperate and arctic ecosystems by has ultimately been attributed to energetic constraints and potential nutrient limitations of other minerals such as phosphorus, molybdenum and iron (Vitousek & Howarth 1991, Uliassi & Ruess 2002). Because most terrestrial ecosystems respond to nitrogen additions by increasing productivity, nitrogen cycling has been intensively studied in both agricultural and natural ecosystems and is relatively well understood (Binkley 2000).

In the interior of Alaska, primary succession occurs on newly exposed terraces formed on silt and gravel bars created by river meander. This bare alluvium has extremely low nitrogen availability. Following the establishment of pioneer willow species (*Salix spp.*) exposed terraces typically accumulate nitrogen rapidly over the first several decades (Walker & Chapin 1986, Kaye et al. 2003, Walker & del Moral 2003). The primary source of this accumulated nitrogen has been attributed to plant communities with symbiotic nitrogen-fixers (Uliassi and Ruess 2002). However, rapid accumulation of nitrogen has also been observed in other semi-arid riparian areas prior

to the establishment of nitrogen-fixers or where nitrogen-fixers are rare (Adair & Binkle 2002, Andersen et al. 2003). The source of this nitrogen is a subject of speculation and has been attributed to a variety of different mechanisms (Klingensmith & Van Cleve 1993, Shade et al. 2001, Adair et al. 2004).

One potential source of nitrogen that has received relatively little attention is uptake of atmospheric ammonia via plant stomata (Hutchinson et al. 1972). Ammonia is a naturally occurring gas found in the atmosphere in low concentrations (Langford & Fehsenfeld 1992). Like CO_2, ammonia enters plants through stomata and then has the potential to diffuse into the interstitial space of the leaves where it is assimilated. This mechanism may not have received consideration for a number of reasons. First, although rates of volatilization can be measured with relative ease with chambers directly at the soil-atmosphere interface, ambient atmospheric ammonia concentration can be difficult to measure and quantify *in situ*. Second, the amount of nitrogen supplied is relatively small in comparison to plant demands of agricultural or commercial forest ecosystems. Finally, high ammonia concentration is typically found in areas heavily impacted by anthropogenic activities, where ecosystem nitrogen saturation is common.

The Bonanza Creek Long Term Ecological Research (LTER) site, interior Alaska, offers an ideal situation for studying the nitrogen dynamics of semi-arid riparian ecosystems. The Tanana River flows through the center of the LTER sites and a primary successional sequence extends across the floodplain, ranging from bare

mineral soil at the banks to dense stands of spruce (*Picea spp.*) on the upper terraces. A wide variety of studies focusing on nitrogen cycling and productivity have been conducted in these sites. Previous measurements of nitrogen availability can not explain the observed productivity found in some of these communities, particularly in the earliest stages of succession (Ruess et al. 1996; Table 1). The apparent discrepancy between plant uptake and nitrogen availability in soils suggests that plants may be using alternate sources of nitrogen.

Despite the lack of anthropogenic influences associated with the Tanana River floodplain, localized environmental conditions may be conducive to high atmospheric ammonia concentration. The soil underlying early successional communities of the Tanana River floodplain is alkaline and characterized by the formation of a calcareous salt crust (Dyrness & Van Cleve 1993). Small areas with large soil ammonium pools could potentially be created by moose (*Alces alces*) urine patches and feces or beneath the nitrogen-fixing alder (*Alnus tenuifolia*) that establish early in succession. Both of these sources coupled with high soil pH create an environment favorable to the volatilization of ammonium, and potentially creating plumes of ammonia to plants growing in nearby environments (Sharpe & Harper 1995).

One promising method of identifying the occurrence of ammonia volatilization is through the use of ^{15}N stable isotopes (Harper & Sharpe 1998). The process of ammonium volatilization is known to cause a strong fractionation of nitrogen isotopes, resulting in the lighter isotope escaping into the atmosphere at a higher rate, leaving the

soil ammonium pool more enriched (Hogberg 1997). The net fractionation from the process of volatilization has been reported to result in ammonia depleted as much as 40‰ (Handley et al. 1996). The tissue of plants absorbing atmospheric ammonia as a substantial source of nitrogen can exhibit depleted $\delta^{15}N$ values as a result. Several recent studies have successfully used ^{15}N isotopes in temperate and sub-Antarctic ecosystems to identify plant communities absorbing ammonia (Erskine et al. 1998, Frank & Evans 1997, Frank et al. 2004). Examining $\delta^{15}N$ of individual plant species across the changes in nitrogen demand and availability associated with succession may help elucidate the role of atmospheric inputs of ammonia in meeting plant nutrient requirements.

In this study we examine the relationship between *in-situ* atmospheric ammonia concentration and patterns of natural isotope abundance. Three hypotheses were tested to determine if atmospheric ammonia was a source of nitrogen to plants along the Tanana River:

H1: Atmospheric ammonia concentration will be highest in the stages of succession dominated by the symbiotic nitrogen-fixer thinleaf alder, where soil nitrogen pools are large and pH is high.

H2: The reliance of individual plant species on atmospheric ammonia will decrease across succession as soil nitrogen availability increases and ammonia concentration decreases.

H3: The magnitude of uptake of atmospheric ammonia by early successional willow communities will depend on the proximity to stands of alder.

In particular, we measured ammonia concentration across five different stages of succession, and stable isotope signatures were used to identify plants using gaseous ammonia. Emphasis was placed on the early successional willow-dominated communities for two reasons: 1) they have the lowest soil nitrogen availability and 2) they are the closest to the potential sources, i.e., stands with high abundances of alder.

Methods

Site Description

The study was conducted within the early successional plant communities of the Tanana River floodplain, at the Bonanza Creek LTER site located about 30 km southwest of Fairbanks, Alaska (64° 48' N, 147° 52' W). The Tanana River forms near the border of Alaska and Canada, and drains a basin approximately 113,920 km^2 in size. Downriver from Fairbanks the Tanana River valley opens to 80-100 km in width, and contains an active floodplain of 300-2000 m across. At the study sites the Tanana River forms of a series of braided channels with sandbars and islands.

Among the first woody plant species to inhabit these sites are a variety of willows (*Salix interior, S. alaxensis*, *S. nova-anglea*, *S. branchycarpa*, *S. lasiandra* and others) and thin-leaf alder (*Alnus tenuifolia*). In later stages of succession, balsam poplar, white spruce and black spruce (*Populus balsamifera*, *Picea glauca*, and *P. mariana*, respectively) dominate the overstory vegetation.

Air temperature ranges from -50 to 25°C, with approximately 100 frost-free days annually. The rain shadow created by the neighboring Alaska Range results in the region only receiving 269 mm of mean annual precipitation, approximately 37% of that is snow (Viereck et al. 1993b). Potential evapotranspiration approaches twice the amount of annual precipitation, implying ground-water and the river act as important sources of water for vegetation. Flooding and an accompanying deposition of sediment occur on a regular basis. The deposition of sediment and changes in the river's channel lead to the development of unvegetated, exposed soil.

Willow is dominant for the first decade of following initial vegetation establishment during which time it is heavily browsed by herbivores. During the period where bare alluvium is exposed, capillary rise creates a substantial salt crust, resulting in alkaline soils. After several years of colonization, a layer of organic material begins to develop at that point evaporation is significantly reduced. As salt content diminishes with reduced capillary rise, and browsing pressure from herbivores continually suppresses the willows, alder begins to play a greater role, and as a nitrogen fixer quickly out-competes the willows. During stand dominance by alder, soil nitrogen pools increase rapidly and provide much of the nitrogen found in later stages of succession.

Atmospheric Ammonia Concentrations

To sample the availability of atmospheric ammonia on the Tanana River floodplain, six transects were selected, each of which ran from the river's edge across the successional gradient from willow to white spruce-dominated communities. The woody vegetation of these communities comprised primarily of a mixture five species: *Salix interior*, *Salix alaxensis*, *Alnus tenuifolia*, *Populus balsamifera*, and *Picea glauca.* Each transect was located on an individual island separated by 1-10 km from the others. Along every transect, 7 to 12 sampling points were established at distances of 20 to 30 m apart, and the successional stage at each point was classified based on the descriptions of vegetation presented in Viereck et al. (1993a). Willow, alder, alder/poplar, poplar, and poplar/white spruce dominated stands were categorized as successional stages III, IV, V, VI and VII respectively. At each sampling point, acid traps were placed to quantify atmospheric ammonia concentration. Acid traps were modified versions of static acid traps commonly used in ammonia volatilization studies (Schlensinger & Peterjohn 1991, Frank & Zhang 1997). Briefly, traps consisted of cylindrical polyethylene containers filled with 5 mL of 4% w/v boric acid, protected by a rain shield, and suspended by a stainless steel wire from an adjacent tree at a height of 0.75 to 1 m above the forest floor for one week from July 20th to July 27th, 2004. An attempt was made to suspend each as close as possible to 1 m, acid traps were hung lower only if no vegetation greater than 1 m in height was present. Following the sampling period, acid traps were capped, wrapped tightly in parafilm, and frozen until

analysis. In the lab each sample was then added to an OPA-sodium sulfite solution and analyzed fluorometerically for ammonia using a FL600 Microplate Fluorometer (Biotek, Woburn, MA)(Holmes et al. 1999). Atmospheric ammonia concentration was calculated according to Tate (2002) by first determining the sampling rate of the trap as follows:

$$r = D \cdot A \cdot L\text{-}1 \qquad [1]$$

Where r = sampling rate ($cm^3 \cdot s^{-1}$)

D = diffusion coefficient of ammonia ($cm^2 \cdot s^{-1}$)

A = Cross sectional area of trap (cm^2)

L = Length of trap (cm)

Once the sampling rate was established, atmospheric concentrations of ammonia were calculate using the equation:

$$C = Q \cdot r^{-1} \cdot t^{-1} \qquad [2]$$

Where C = atmospheric ammonia concentration ($ug \cdot m^{-3}$)

Q = ammonia absorbed (µg)

t = deployment duration (s)

This calculation uses a mean coefficient of diffusion for ammonia taken from the literature, and assumes the trap (i.e. boric acid) is an indefinite sink. A short deployment period and relatively large volume of acid were used to help ensure the validity of this assumption.

Using standard laboratory procedures (Robertson et al. 1999) soil pH was measured in the summer of 2001, at 18 locations within each of four of the five successional stages.

Natural Abundance of $\delta^{15}N$ Across Succession

Natural abundance of $\delta^{15}N$ was used to identify plant species with depleted isotopic signatures suggestive of stomatal uptake of volatilized ammonia. At each site along the transects leaves were collected from each woody species. Leaves were randomly sampled from 1-4 plants (10-20 leaves per plant) at each site with the number of plants sampled depending on the abundance of the given species (i.e., if four or more plants of a species were present, leaves from were collected from 4 individuals, and if less than four were present leaves were collected from each individual). All of the leaves for an individual species at a given point were composited. The leaves were brought to the laboratory, dried for 48 hours at 65° C, and ground to a fine powder using a ball mill. At each site along each transect a single soil core was taken to a depth of 15 cm, including the organic horizon where present, but excluding litter and moss layers. The soil was homogenized, dried at 65° C for 48 hours and ground to a fine powder using a ball mill. Leaf and soil samples were then analyzed for % nitrogen and $\delta^{15}N$ using a continuous flow mass spectrometer (PDZ Europa, Inc., Cheshire, UK).

$\delta^{15}N$ values of Early Successional Willow Communities

Two early successional sites (< 5 yrs) were established at each of two locations along the Tanana River floodplain; two were near the LTER site FP1B and two were located on Deborah's Island. Both locations were on large islands typical of the lower terraces of the floodplain, and each island was also the location of one of the six transects mentioned in the previous section. The four sites were categorized into low, intermediate and high alder densities as follows: The downriver plot at FP1B had an high density of alder and the upriver plot had an intermediate density of alder. The high density plot was situated in a narrow swath, approximately 40 m wide, between two dense stands of alder, and the intermediate density plot was located at the mouth of this swath, so that dense stands were relatively close downriver, and upriver there were only willow stands. On Deborah's Island, there was alder within about 50 m of the upriver plot, and only a few individual alder were in the general area; the upriver plot was designated a low alder density. The downriver plot on Deborah's Island had no alder within about 50 m but had a small stand of alders beyond that; it was classified as an intermediate density. Each plot was 10 m x 3 m and divided into a grid of ten sub-plots. 3-5 leaves were collected from every willow within each sub-plot, composited, and taken to the lab where they were dried at 65° C for 48 hours, and then ground to a fine powder. Soil samples were collected at three points within each sub-plot at depths of 0-25 cm, 25-50 cm and 50-75 cm. Soils were composited by depth within each sub-plot, dried at 65° C for 48 h, ground to a fine powder and analyzed following the

methods outlined in the paragrapth above. Both plant tissue and soil were then analyzed for %N and $\delta^{15}N$ following the methods in the paragraph above.

Results

Atmospheric Ammonia Concentrations

Atmospheric ammonia concentration ranged from <0.1 to 160 $\mu g \cdot m^{-3}$. The overall mean across all six transects was approximately 10.4 ± 2.3 $\mu g \cdot m^{-3}$. There was a trend showing mean ammonia concentration to be highest in the willow and alder stages, and then decreasing across the successional sequence (Figure 1). However no statistically significant differences were found in ammonia concentration among successional stages along the transects (Analysis of Variance {ANOVA}, n=34, α = 0.05). Power analysis, using the range in concentration observed in this study as an estimate of variance, showed future studies would need to have a sample size of $n > 80$ sites to test differences of 3 $\mu g \cdot m^{-3}$ at $\alpha = 0.05$ and power of 0.80. The pattern of ammonia concentration coincided with changes in soil pH along the successional gradient (Table 2).

Natural Abundance of $\delta^{15}N$ Across Succession

Across the species in this study, $\delta^{15}N$ values for leaf tissue ranged from approximately -9 ‰ to 0 ‰. Within species, as much as a 5 ‰ range was observed

among successional stages, with variation of 2 ‰ to 5‰ in poplar, white spruce, and *S. alaxensis* leaves, and less then 2 ‰ in alder and *S. interior*. Linear regression (α = 0.05) showed no statistically significant relationships between leaf $\delta^{15}N$ values and atmospheric ammonia concentration for any of the five species or for soil $\delta^{15}N$ values. Despite the lack of a statistical significant relationship, *S. alaxensis* and alder both followed an inverse trend to that observed in pH and atmospheric ammonia concentration, becoming more depleted in $\delta^{15}N$ as ammonia and pH increased (Table 2). These trends support the idea of depleted ammonia volatilizing in areas of high pH, and being assimilated into leaf tissue.

Total nitrogen concentration in soil ranged from <0.01 % (below detection) to 0.20 %, and mean values increased across succession from 0.04 % in the willow stage to 0.11 % in the later stages. A substantial number of soil $\delta^{15}N$ samples that contained too little nitrogen to yield reliable isotopic ratios, and were thus excluded from the study. $\delta^{15}N$ values of *S. alaxensis* foliage and nitrogen concentration in soil were significantly correlated (Figure 2). Depletion of the isotopic signatures of *S. alexansis* foliage as soil nitrogen content decreases follows with the hypothesis of a shift toward reliance on ammonia when soil has low nitrogen availability. *S. alaxensis* also showed a significant relationship between foliar $\delta^{15}N$ values and leaf nitrogen concentration (Figure 2). The plants with higher nitrogen levels in their leaves do not appear to be dependent on a source of depleted ^{15}N.

$\delta^{15}N$ of Early Successional Willow Communities

For FPB1 and Deborah's Island, mean concentrations of ammonia were calculated by taking the average ammonia values across the transects that spanned the respective islands. The woody vegetation of all four plots was *S. interior*. A 2 ‰ difference in $\delta^{15}N$ values for *S. interior* leaves was observed among plots at FPB1, and a 3 ‰ difference was observed among plots at Deborah's Island. Overall there was a 5.5 ‰ range in $\delta^{15}N$ across the four plots. A significant difference was observed between the two islands in both foliar and soil $\delta^{15}N$ values (ANOVA, $n = 31$, $\alpha = 0.05$), as well as among all four locations (Tukey's multiple comparisons, $n = 31$, $\alpha = 0.05$). There was a significant relationship between both soil and foliar $\delta^{15}N$ and density of nearby alder (Figure 3). Both trends were consistent with the overall concept of ammonia volatilization and stomatal uptake.

Discussion

Plant Uptake of Atmospheric Ammonia

Atmospheric ammonia is a well documented source of nitrogen for plants (Hutchinson et al. 1972, Langford and Fehsenfeld 1992, Sutton et al 1995, Frank et al. 2004). However, relatively few studies have examined atmospheric ammonia in comparison to the number of studies focusing on soil nitrogen dynamics, and fewer still have attempted to examine it on an ecosystem scale context. This is the first study to address the role of atmospheric ammonia in a successional framework, and to examine

its importance to early successional boreal ecosystems. This is also the first study to suggest atmospheric ammonia as a potential source of the common occurrence of depleted $\delta^{15}N$ values in plants occurring within high latitude ecosystems with small nitrogen inputs.

Forests can act as both sources and sinks for atmospheric ammonia. Langford and Fehsenfeld (1992) calculated a mean compensation point of 0.6 $\mu g \cdot m^{-3}$ for a sub-alpine montane forest; below this concentration the forest acted as a source for atmospheric ammonia, when the concentration exceeded this value the forest acted as a sink. Similarly the compensation point for spruce forests in Germany was calculated to be 0.3 $\mu g \cdot m^{-3}$ (Kesselmeier et al 1993). If comparable compensation points exist for the sub-arctic plant communities in this study, then even the lowest mean ammonia concentration recorded exceeded those compensation points. Although most measurements fell around mean values reported, about 10 % of the locations measured had atmospheric concentrations equal to or exceeding 40 $\mu g \cdot m^{-3}$ suggesting that there are potential "hotspots" across the landscape. The temporal and spatial variation associated with these hotspots would be influenced by an assortment of biotic and abiotic factors. Thus the measurements reported here represent an approximate set of snapshots of the atmospheric ammonia on the Tanana floodplain.

Sources of Depleted $\delta^{15}N$

All species, with the exception of alder, exhibited substantial variation in foliar $\delta^{15}N$ values. The results from transects suggest that *S. alaxensis* was using depleted atmospheric ammonia when soil nitrogen is limiting. This is consistent with other research showing the amount of ammonia absorbed by plants is a function of both atmospheric concentration and the degree of plant nitrogen-limitation (Harper and Sharpe, 1998). The intensively sampled *S. interior* sites indicate that these communities may be using atmospheric ammonia also, showing a distinctive pattern with soil becoming increasingly enriched, and foliage depleted, as alder proximity increases.

Natural abundance of stable nitrogen isotopes can act as an integrated indicator of the nitrogen dynamics that a plant or plant community experiences. Data from this study show a rather unusual 10 ‰ shift within single species across a spatial area <5 km in size. However, large variation and depleted $\delta^{15}N$ values among arctic and sub-arctic plants is not an unexpected phenomenon. Nadelhoffer et al. (1996) observed 10‰ variation across 12 arctic species in a variety of ecosystems spread over a transect 800 km in length. Likewise, highly depleted values have been observed in foliar tissue of many high latitude plant species (Michelsen et al. 1996). These past studies attributed the depleted signatures to the mycorrhize associated with different species, but did not observe or address shifts in $\delta^{15}N$ within species. In comparison to non-mycorrhizal species, some mycorrhizal species displayed significantly depleted $\delta^{15}N$ values, but the causality has yet to substantiated; neither the relative enrichment of fungal tissue in

these mycorrhizal associations, nor the observed rates of fractionation have adequately explained the level of depletion observed (Hogberg 1997, Dawson et al. 2002).

Several lines evidence support the conclusion that the $\delta^{15}N$ values observed in this study are not a sole function of mycorrhizal associations. First, the studies focusing on differences in $\delta^{15}N$ values associated with mycorrhize have compared differences in the isotopic signature between groups of species with differing mycorrhizal associations (Nadelhoffer et al. 1996, Michelsen et al. 1996, Michelsen et al. 1998). Using the same system of categorization as these previous studies the individuals of each separate species would be grouped together, suggesting the variation observed within species does not result from fundamental differences in mycorhizzal associations. Second, the depleted signature associated with mycorrhize is believed to be a function of their ability to absorb organic forms of nitrogen typically unavailable to plants (Michelsen et al. 1996, Dawson et al. 2002). These organic sources of nitrogen are thought `to have a more depleted isotopic signature than mineral sources of nitrogen. The willow dominated communities in this study that are the most likely to display the depleted $\delta^{15}N$ values associated with atmospheric ammonia uptake are characterized by the absence of a forest floor, and small amounts of organic material implying mycorrhizal associations would be playing a relatively minor role in nitrogen supply compared to other ecosystems (VanCleve et al. 1993a). Finally, if the values of adjacent upland populations of *S. alaxensis* are taken into consideration, there is a 7‰ difference in $\delta^{15}N$ (Kielland et al. 1998), which is at the extreme end of the range of values (0 to 7.7‰)

(Michelsen et al. 1998, Dawson et al. 2002) reported in literature for differences between mycorrhizal and non-mycorrhizal species, and substantially larger then the within-species range (± 0.01‰) between individual *Pinus sylvestris* plants infected and uninfected by mycorrhize (Hogberg et al. 1999).

Conclusion

The potential for ammonia volatilization and subsequent plant uptake and assimilation via stomata exists in any ecosystem, especially those that have both high soil pH's and high nitrogen availability. Because ammonia in plants with adequate nitrogen supply can volatilize from the leaves, where nitrogen is abundant the signature from atmospheric uptake may be masked and thus easy to overlook. Intrinsically low levels of nitrogen availability may increase the sensitivity of $\delta^{15}N$ values as indicators of ecosystem function in nitrogen-limited communities.

Frank and Evans (1997) reported a depleted signal in leaf tissue of plants grow outside compared to inside a series of 40 ha herbivore exclosures in Yellowstone National Park. Recently they have shown that simulated urine patches led to both large amounts of ammonia volatilization, and localized depletion of $\delta^{15}N$ values of grass shoots in the area (Frank et al. 2004). Based on rates of ammonia uptake in soybeans in the laboratory, Hutchinson et al. (1972) calculated that atmospheric ammonia at concentrations of 30 $\mu g \cdot m^{-3}$ would equate to a supply of 20 kg $N \cdot ha^{-1}$ annually. This is approximately 6 to 10 times the amount of nitrogen being made available in the early

stages of succession at these sites through soil microbial processes (Van Cleve et al. 1993, Kielland unpublished data). The mean ammonia concentrations for the early stages of succession were approximately 14 $\mu g \cdot m^{-3}$, and, if the plants in these communities absorbed ammonia at a similar rate to that observed by Hutchinson, atmospheric uptake of ammonia could account for over 80 % of annual growth requirements. Although the comparison of a field of soybeans to a primary successional willow community is tenuous at best, even if rates of stomatal conductance vary by an order of magnitude between the two ecosystems, atmospheric ammonia would still be an important contributor to annual nitrogen supply. When coupled with our understanding of plant physiology and nitrogen chemistry, the evidence presented here warrants the consideration of stomatal absorption of ammonia as an important mechanism for nitrogen supply, especially in low nutrient environments and other ecosystems where nitrogen is accumulating at rates that defy conventional measurements.

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Table 1. Patterns of nitrogen accumulation across four stages of primary succession. All data is present as $g \cdot m^{-2} \cdot y\text{-}1$. Constructed using data from 1. Van Cleve et al. 1993, 2. National Atmospheric Deposition Program data 2002, 2003 & 2004, 3. Klingensmith and Van Cleve 1993, 4. Uliassi and Ruess 2002, 5. Ruess et al. 1996, 6. Walker and Chapin 1986, 7. Viereck et al. 1993 and 8. Ruess et al. 2004.

Total Measured Nitrogen Inputs

Stage	Nitrogen Mineralization[1]	Nitrogen Deposition[2]	Nitrogen Fixation[3,4,5]	Total N Input
III-Willow	0.25	0.08	0.10	0.43
V-Alder	1.50	0.08	6.72	8.30
VI-Poplar	1.60	0.08	2.20	3.88
VIII-White Spruce	1.00	0.08	0.15	1.23

Annual Plant Nitrogen Requirements

Stage	Aboveground N Requirements[6,7]	Belowground N Requirements[6,8]	Total N Requirements	% N Requirement Supplied
III-Willow	1.12	0.51	1.63	26
V-Alder	4.34	2.05	6.39	130
VI-Poplar	1.78	3.04	4.82	81
VIII-White Spruce	1.47	1.63	3.10	40

Table 2. Soil and foliage δ15N values, atmospheric ammonia concentrations, and pH across succession.
Data are presented as means ± **SE**. Letters denote differences between means within each column as determined by Tukey's Multiple Comparisons at $\alpha = 0.05$.

Dominant Vegetation	δ^{15}N Soil (‰)	δ^{15}N *S. interior* (‰)	δ^{15}N *S. alaxensis* (‰)	δ^{15}N *A. tenuifolia* (‰)	δ^{15}N *P. balsamifera* (‰)	δ^{15}N *P. glauca* (‰)	NH_3 (µg/m3)	pH
Willow	-0.82 ± 0.67 a	-3.51 ± 0.73 a	-4.82 ± 0.49 a	-1.55 ± 0.11 ab	-5.38 ± 0.28 a	-5.48 ± 0.01 a	14.23 ± 5.26 a	8.01
Alder	-1.22 ± 0.49 a	-5.03 ± 0.52 a	-4.56 ± 1.02 a	-1.64 ± 0.15 a	-4.98 ± 0.44 a	N/A	11.97 ± 5.29 a	8.1
Alder & Poplar	-0.19 ± 0.40 a	-5.35 ± 0.68 a	-3.70 ± 1.58 a	-1.39 ± 0.08 ab	-5.22 ± 0.56 a	-5.82 ± 0.82 a	8.21 ± 4.60 a	N/A
Poplar	0.47 ± 0.54 a	-4.82 ± 0.01 a	-2.94 ± 2.93 a	-1.15 ± 0.09 b	-6.87 ± 0.24 b	-5.57 ± 0.49 a	3.55 ± 1.50 a	6.7
White Spruce	-1.30 ± 1.93 a	N/A	-2.93 ± 2.00 a	-1.20 ± 0.10 ab	-5.05 ± 0.63 a	-7.67 ± 0.85 a	5.31 ± 2.78 a	6.1

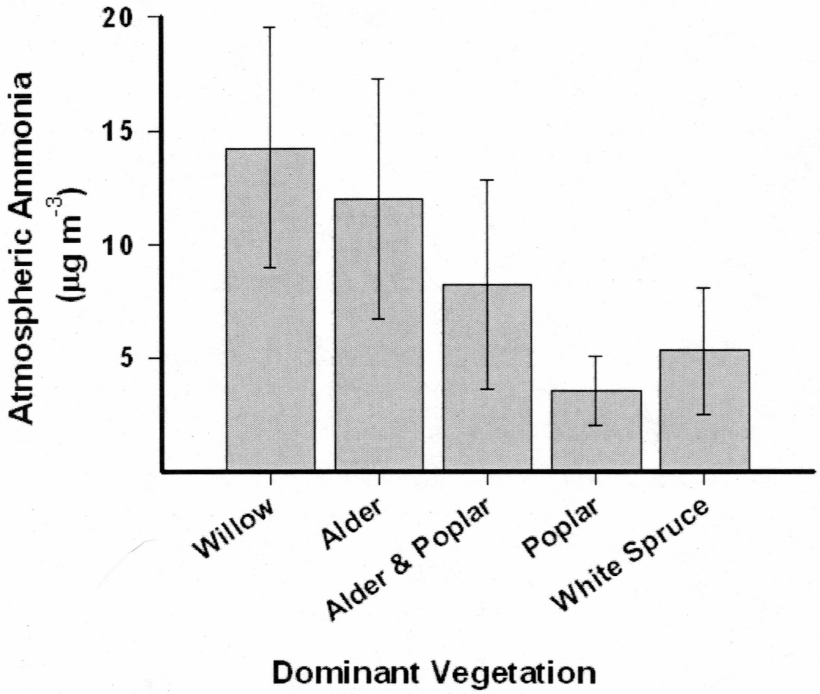

Figure 1. Atmospheric ammonia concentrations along the Tanana River floodplain. Average ammonia concentrations for the first five woody plant communities along the primary successional sequence of the Tanana River Floodplain. Data means ± **SE**.

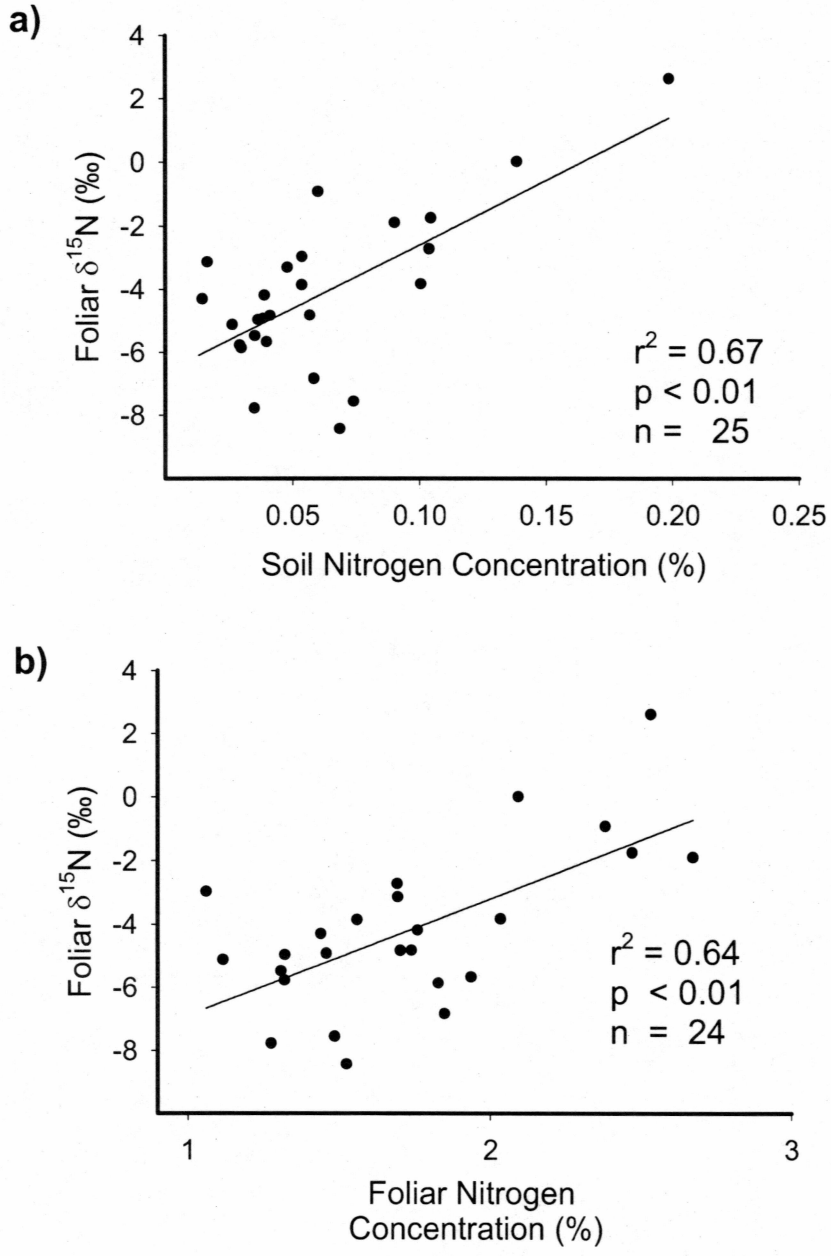

Figure 2. The relationships between *S. alexansis* foliage $\delta^{15}N$ natural abundance and indices of nitrogen availability.

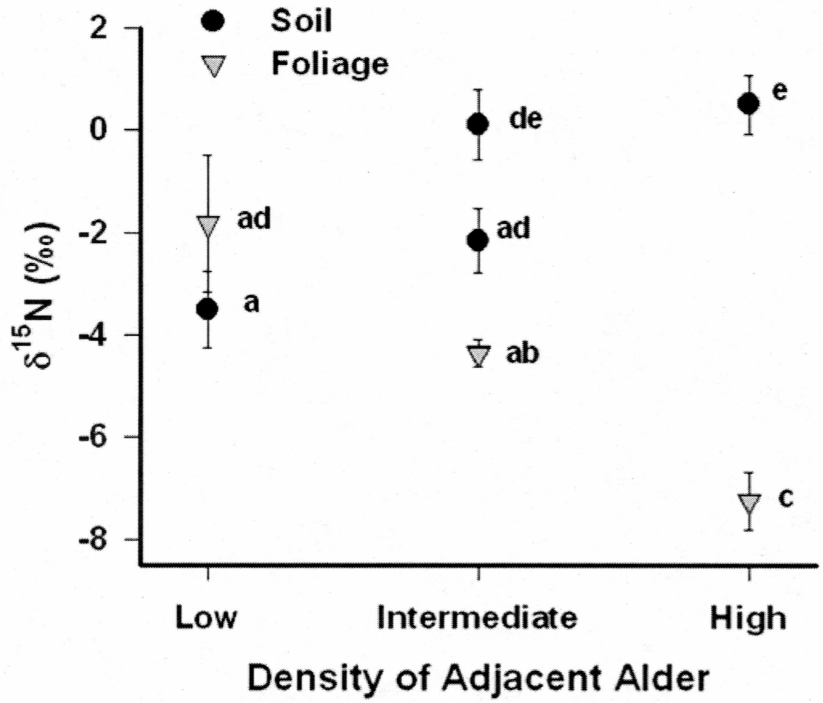

Figure 3. *S. interior* foliage and soil δ^{15}N values in relation to the relative abundance of thinleaf alder in the immediate vicinity. Data are means ± **SE**. Letters denote differences between means determined by Tukey Multiple Comparisons at $\alpha = 0.05$ and $n = 34$.

IV. General Conclusions

Semi-arid riparian areas are separated from other forest ecosystems by a variety of unusual characteristics. A variety of other factors influence the nitrogen cycle in addition to the normal controls of nitrogen availability. Along the Tanana River fluvial dynamics greatly affect the soil environment supplying nutrients to microbes and roots, and potentially stimulating productivity. Capillary rise carries water and solutes from the underlying water to the unsaturated portion of the rooting zone during the drier portions of the year. If all of these processes are taken into consideration they account for more than 80 % of the annual nitrogen requirements for above-ground plant productivity. Additional periods of saturated flow early in the summer during snow melt and break-up could also contribute a significant amount of nutrients.

In addition to nitrogen, capillary rise also deposits large quantities of dissolved salts to the surface soils of these sites. This process may set the stage for substantial quantities of ammonia volatilization in later stages of succession, by increasing the pH of the surface soil. When ammonium is added to these soils, by either contribution from thinleaf alder or waste products from animals, ammonia volatilization will occur. If the local concentrations become high enough ammonia in the atmosphere then becomes a viable source of nitrogen for plants growing in the vicinity. Our estimates place the quantity absorbed at explaining anywhere from 3 to 100 % of the annual nitrogen needed for plant productivity. More research would be needed to definitively assess the importance of this mechanism; however, this study should serve as a

reminder that the $\delta^{15}N$ can be a powerful indicator of ecosystems processes when used in the proper context.

Both of the alternative mechanisms of nitrogen supply examined in this study have the potential to meet or exceed supply from conventional sources. Although science has evolved to the point that regional and global scale predictions of biogeochemical processes can be made with a fair degree of accuracy, extending this knowledge to make predictions in specific ecosystems still presents a challenge. This is exemplified in environments that are complex, heterogeneous, and dynamic, such as floodplains and other riparian areas. Unraveling these complex interactions is key to completing our understanding of ecosystem function, and is critical to making sustainable management decisions.

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